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Slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in arid parts of Washington

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It is a well-known fact that the vegetation on hills and mountain slopes differs according to the exposure of the locality to different quarters of the compass. A flora of mainly xerophytic character inhabits the south-facing slope, while the northern declivity, less exposed to insolation, is covered with a more or less mesophytic vegetation. Also the southwest and southeast slopes are generally occupied by a xerophytic flora, the northeast and northwest by a mesophytic.

The great differences in the distribution of plant-communities as well as individuals due to variations in insolation may be seen in every part of the world. Warming (10, 11) tells us how in Greenland the southern slopes of a mountain chain may have an open xerophytic vegetation "appearing as if burnt up," while the northern slopes are at the same time covered by a dense, green, mossy carpet, with many flowering plants. The same may be observed in the Mediterranean countries, and even in the proximity of the equator we find a marked distinction between the flora of the northern and southern slopes.

But slope exposure is an important factor not only in the determining of different types of vegetation over wide areas; it also affects the vegetation within a very limited area. Giltay (3) has shown how a great difference may exist between the temperature and atmospheric humidity on the northern and southern slopes respectively of the sand-dunes in Holland, even when only a few paces apart. More recently Stenström (4) investigated the difference in the flora of the embankments of railways, showing how some plants occupy the southern embankment, others the northern, etc.

While studying the influence of slope exposure upon the distribution of the various plants on the banks of Spokane River in eastern Washington the writer's attention was particularly directed

to the behavior of *Pseudotsuga taxifolia*, popularly known as Douglas spruce. The range of this conifer is extensive. It is found most luxuriant in the Vancouver strip, reaching perhaps its highest development in the Puget Sound region (see also Sudworth, 9). This region, falling within the limits of Merriam's Humid Transition area (5), is notable for its moist climate favoring a luxuriant growth of dense forests, almost exclusively composed of Douglas spruce, which here assumes gigantic dimensions. Less conspicuous and never attaining the development it reaches in the Vancouver strip, it reappears in the extreme eastern part of Washington and in northern Idaho where the climatic conditions approach those of the coast region. The main distribution of the tree in this region seems to coincide with the Canadian Zone of Merriam.

Abundance of moisture in atmosphere and soil seems to be of vital importance to the growth of Douglas spruce. It is therefore surprising to find this conifer occupying the drier parts of eastern Washington, Merriam's Arid Transition area. Realizing the scanty rainfall—about 18 inches in Spokane—it may well be questioned how the tree is able to endure the extremities to which Humid Transition plants are submitted in this arid region. The problem loses some of its complexity when it is found that Douglas spruce in this region always occupies the shady northern slope of hills and ridges, and is entirely absent on the southern, thus affording a most notable example of the effect of slope exposure. Nowhere is this more beautifully shown than on the banks of Spokane River in the vicinity of Spokane. The banks, composed of glacial detritus, sometimes attain a height of 50 meters, and the vegetation of the sunny south-facing bank is in striking contrast with that of the more shady north-facing bank. This latter is occupied by a pure growth of *Pseudotsuga taxifolia*. A small belt of *Populus trichocarpa*, *Alnus tenuifolia*, *Cornus stolonifera* and *Salix Scouleriana* fringes the edge of the river. The following herbs are common in this belt:

*Artemisia ludoviciana**

Aster foliaceus frondeus

Aster Douglasii

Aster laevis Geyeri

* In questions of nomenclature Piper's Flora of the State of Washington (6) is followed.

<i>Aster oreganus</i>	<i>Scutellaria lateriflora</i>
<i>Heracleum lanatum</i>	<i>Senecio hydrophilus</i>
<i>Impatiens biflora</i>	<i>Solanum Dulcamara</i>
<i>Mentha canadensis borealis</i>	<i>Stachys palustris</i>
<i>Roripa Nasturtium</i>	<i>Steironema ciliatum</i>

Higher up on the steep slope, where *Pseudotsuga* becomes dominant, the vegetation shows the following composition:

TREES

Pseudotsuga taxifolia

SHRUBS

<i>Ceanothus sanguineus</i>	<i>Schizonotus discolor</i>
<i>Opulaster pauciflorus</i>	<i>Spiraea corymbosa</i>
<i>Sambucus glauca</i>	

HERBS

<i>Antennaria rosea</i>	<i>Geranium viscosissimum</i>
<i>Arnica cordifolia</i>	<i>Heuchera cylindrica</i>
<i>Campanula rotundifolia</i>	<i>Hieracium albiflorum</i>
<i>Castilleja miniata</i>	<i>Hieracium Scouleri</i>
<i>Claytonia linearis</i>	<i>Mertensia oblongifolia</i>
<i>Claytonia perfoliata</i>	<i>Pentstemon confertus</i>
<i>Claytonia sibirica</i>	<i>Ranunculus glaberrimus</i>
<i>Collinsia tenella</i>	<i>Sedum stenopetalum</i>
<i>Crepis barbigera</i>	<i>Sieversia ciliata</i>
<i>Crepis gracilis</i>	<i>Silene Douglasii multicaulis</i>
<i>Disporum majus</i>	<i>Synthyris rubra</i>
<i>Dodecatheon puberulum</i>	<i>Tellima parviflora</i>
<i>Drymocallis Convallaria</i>	<i>Tellima tenella</i>
<i>Erigeron speciosus</i>	<i>Trillium petiolatum</i>
<i>Erythronium grandiflorum</i>	<i>Vagnera amplexicaulis</i>
<i>Fragaria platypetala</i>	<i>Valerianella macrocera</i>
<i>Galium Aparine</i>	<i>Vicia americana</i>
<i>Galium boreale</i>	<i>Viola adunca</i>
<i>Gentiana oregana</i>	<i>Viola retroscabra</i>

As easily seen, the herbaceous vegetation is made up of truly Transition or Arid Transition plants with one exception, *Claytonia*

perfoliata, a Humid Transition plant here having an isolated station. The formation is of a somewhat open character, but in deeper shade the ground is generally covered by a continuous mat of mosses. Epiphytic lichens are common. On the steep declivity no humus has been able to accumulate, and it is only on the lower part of the bank that a rather thick layer of humus is to be found, owing its existence to the mass of dead matter which is in continuous downward motion.

The opposite south-facing bank has a very different flora; in fact, the contrast is so striking as to make it seem almost unnatural. The heavily *Pseudotsuga*-forested north-facing slope faces a vegetation on the opposite bank, which in xerophily rivals the desert flora! The greater part of the bank is devoid of trees. *Populus trichocarpa* fringes the edge of the river, but *Alnus tenuifolia* has disappeared. Shrubs of quite different kind from those in the corresponding belt of the northern bank form the undergrowth. The shrubs are:

<i>Amelanchier florida</i>	<i>Prunus demissa</i>
<i>Clematis hirsutissima</i>	<i>Ribes aureum</i>

The dominant herbs at the water-edge are:

<i>Artemisia ludoviciana</i>	<i>Coleosanthus grandiflorus</i>
<i>Asclepias mexicana</i>	<i>Euthamia grandiflora</i>
<i>Aster laevis Geyeri</i>	<i>Steironema ciliatum</i>
<i>Aster oregana</i>	

The declivity proper has two very marked belts, a lower closed formation, and an upper and open formation, the difference being largely due to the obvious fact that the lower zone is more sheltered against insolation and drying winds than is the upper. A continuous turf of various grasses covers the lower belt, and many of the plants recorded in the list from the northern slope reappear in this relatively sheltered zone. More or less dominant are the following additional:

<i>Apocynum androsaemifolium</i>	<i>Erysimum asperum</i>
<i>Astragalus Purshii</i>	<i>Lomatium triternatum</i>
<i>Delphinium Menziesii</i>	<i>Sphaeralcea rivularis</i>

The most remarkable feature of this zone, however, is the

abundance of shrubs. They do not form thickets, but are scattered widely apart over the area. In some cases, however, one of them, *Berberis repens*, may form a pure growth of some extent. The stratum of shrubs is composed of:

<i>Amelanchier Cusickii</i>	<i>Philadelphus Lewisii</i>
<i>Berberis repens</i>	<i>Rhus Toxicodendron</i>
<i>Crataegus brevispina</i>	

The remaining part of the bank, the upper zone, is by far the most interesting one. As said before, no continuous turf of vegetation is found, only scattered individuals often several feet apart. The intense insolation and the exceedingly dry winds which are so common in eastern Washington in the summer months must be considered as the chief causes for this scanty xerophytic vegetation. Another factor, which may play some part in the difficulty of establishing a closed formation, is the mobility of the substratum. Owing to the steepness of the bank, gravel is rapidly moving downward. Many plants which probably are able to withstand the strong insolation are unable to get a foothold, thus giving room to other plants more adapted to the moving substratum, but poor in the formation of a continuous turf. That many of these plants show a high degree of adaptation to the habitat is evident from the fact that they do not occur outside of these south-exposed banks. The formation, which includes many of the most decorative and at the same time the rarest plants in Spokane Valley, shows a composition of the following nature:

SHRUBS

<i>Ramona incana</i>	<i>Rhus glabra occidentalis</i>
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HERBS

<i>Allocarya hispidula</i>	<i>Eriogonum niveum</i>
<i>Carduus undulatus</i>	<i>Eriophyllum lanatum</i>
<i>Chaenactis Douglasii</i>	<i>Cilia aggregata</i>
<i>Collomia grandiflora</i>	<i>Lappula ciliata</i>
<i>Cuscuta californica*</i>	<i>Lithospermum ruderales</i>
<i>Eriogonum compositum</i>	<i>Lomatium Grayi</i>
<i>Eriogonum heracleoides</i>	<i>Lupinus Piperi</i>

* Infesting *Scutellaria grandiflora*.

<i>Machaeranthera canescens</i>	<i>Phacelia heterophylla</i>
<i>Mentzelia laevicaulis</i>	<i>Physaria Geyeri</i>
<i>Mentzelia integrifolia</i>	<i>Ptiloria exigua</i>
<i>Oreocarya sericea</i>	<i>Scutellaria grandiflora</i>

The vegetation of the upper belt of the south-exposed bank, as recorded in the above list, corresponds closely to the Upper Sonoran flora, to follow Merriam's terminology. In Washington the Upper Sonoran life area is confined to the interior southern part of the State with a rainfall less than 10 inches. However, many of the Upper Sonoran plants follow the valley of Columbia River and its tributaries, and extend far up in the Arid Transition Area. Through the valley of Okanogan River they even reach British Columbia. The warm and sunny south-facing slope of the river banks is well fitted to support this vegetation of a more southern character. They all exhibit xerophily, protecting them from desiccation. A well-developed coating of hair is the most common means of protection, reaching an extreme development in such forms as *Eriogonum niveum* and *Eriophyllum lanatum*, which have a thick felt on leaves as well as stem. One of the forms included in the above list is of more than common interest, namely, *Physaria Geyeri*. This beautiful crucifer is known to occur only in the upper region of Spokane Valley, here usually occupying the southern river banks. The dense coating of hair is apparently a very effective means for depressing transpiration, but it also constitutes, in connection with the cushion-like and tufted character of the plant, a method of protection against the low winter temperature. Flowering in the latter part of April and the whole month of May, refluorescence very often takes place in August, and this refluorescence lasts often through all winter. A few hours of sunshine even in the most severe winter months, December and January, is enough to induce it to open its yellow flowers.

Where the slope terminates upwards and level ground commences this characteristic flora ceases abruptly, and the dry *Pinus ponderosa* forest with its scanty undergrowth takes its place. In some places where the slope is gentle it merges into the flora of the gravelly prairie dominated by *Balsamorhiza sagittata* and *Gaillardia aristata*.

From the above we find how profoundly slope exposure in-

fluences, and how it determines, the kind of vegetation present. Coming back to *Pseudotsuga taxifolia* the evidences have showed that exposure is the regulating factor in the distribution of the tree in this region, the northern slopes and ridges being the only localities which offer the needed humidity in soil and atmosphere. Not only around Spokane but in all more or less arid regions can this be observed. Piper (6) cites the example of Kamiak Butte, a granitic cone in the arid region of eastern Washington projecting about 500 meters above the surrounding basalt, having its entire south exposure covered by a bunchgrass flora, while the northern slope is densely timbered with yellow pine and other coniferous trees (including *Pseudotsuga taxifolia*). Even in regions with a higher amount of annual precipitation, as in the extreme eastern part of the State and in northern Idaho, we find *Pseudotsuga* by far better developed on the northern exposure, though lacking in the more moist situations, not being able to compete successfully with *Thuja plicata*, which here becomes dominant. At a higher altitude, mainly in the Canadian zone, it again becomes the dominant tree on the northern slopes, while *Pinus contorta* often becomes the most conspicuous on the southern exposure. Watson (12) describes a similar case from north central New Mexico, in which region *Pseudotsuga taxifolia* covers the north-facing slopes above 8,000 feet (the Canadian Zone) and extends down in the narrow canyons to about 7000 feet.

Turning now our attention to the distribution of *Pseudotsuga taxifolia* in the dry regions of western Washington, we find it growing in the San Juan Islands. These islands, situated between the Strait of Juan de Fuca and the Strait of Georgia, are remarkable for their dry climate and for the many Arid Transition plants which there have been able to get a foothold, since the climatic conditions resemble those in eastern Washington. The nature of the climatic conditions may best be illustrated by mentioning that the only cactus which occurs in the Vancouver strip, *Opuntia polyacantha borealis*, is confined to one of these islands. Other truly Arid Transition plants are also found, for instance *Sieversia ciliata*, *Polemonium micranthum*, *Lupinus microcarpus* and *Juniperus scopulorum*. The problem is a somewhat puzzling one, and Piper (6, p. 44) remarks: "Only one physical factor

presents itself which may explain these strange cases, namely, the fact that these islands lie in the lee of the Olympic Mountains and therefore have a lesser rainfall. The conditions, therefore, more nearly approximate those of the Arid Transition area than any other portion of Washington west of the Cascade Mountains." It is not surprising to find *Pseudotsuga taxifolia* confined to the northern slopes of the hills in these islands; in fact, a different behavior would be hard to understand, since it is here submitted to practically the same climatic conditions as in other arid regions of its range, where it, as has been shown, always occupies the northern declivity as a result of the effect of slope exposure.

Rigg (7) has in an interesting paper, dealing with the forest distribution in these islands, pointed out the seemingly peculiar distribution of *Pseudotsuga taxifolia* as limited to the north-facing slopes of the hills. He is inclined to attribute to the soil the difference in the forest distribution. Upon investigation of the soil on the barren south-facing slope and on the forested north-facing, it was shown that the soil on the barren portion was black and powdery, containing a good deal of gravel, while the forested portion was everywhere covered with two feet or more of yellow clay, containing occasional irregular fragments of rock.

It is hard to believe that the chemical nature of the different soils should cause the difference in the forest distribution, but as darker soil is more readily and strongly heated than is that of lighter color, this character may in a subordinate way have some influence (see Falk, 2; Schimper, 8; Warming, 11). When we on the other hand know how profoundly slope exposure affects the distribution of *Pseudotsuga taxifolia* in regions with similar climatic conditions to those in the San Juan Islands, the determining factor is presumably the same.

Cowles (1) no doubt is right when stating that a species in general can grow in a large number of formations at its center of distribution, since there the climatic condition favors it most highly. In other regions, especially near its areal limits, it can grow only in those formations which resemble most closely in an edaphic way the climatic feature at the distribution center. We have found how *Pseudotsuga taxifolia* when growing under conditions not favorable to its development always establishes itself

on north-facing slopes and banks, and thus secures the greatest possible amount of atmospheric and telluric moisture.

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